THE EOCENE NORTH ATLANTIC LAND BRIDGE: ITS IMPORTANCE IN TERTIARY AND MODERN PHYTOGEOGRAPHY OF THE NORTHERN HEMISPHERE[1]

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THE TRANSITION from the Cretaceous to the Tertiary marks a time of significant modernization in the history of flowering plants. During this interval, a wide range of extant families and genera first appeared, as recorded in the fossil record of pollen (Muller, 1970, 1981) and fruits and seeds (Tiffney, unpubl. data). This modernization was probably spurred by coevolution with pollinators (Crepet, in press) and dispersal agents (Tiffney, in press) and resulted in a major change in the floristic and vegetational composition of the world's plant communities.

Concomitant with this modernization, the newly evolved taxa spread rapidly over the Northern Hemisphere (Wolfe, 1975) during a period of equable climate (Kennett, 1977; Savin, 1977; Buchardt, 1978; Wolfe, 1978) to form a hemispheric flora. This flora seems unusual by modern standards since it consisted of a mixture of taxa, the modern counterparts of which are found in habitats ranging from deciduous northern hardwood forests (e.g., *Juglans* L., *Carpinus* L., *Betula* L.) to tropical and paratropical rain forests, particularly of southeastern Asia and Malaysia (e.g., *Nypa* Steck, *Mastixia* Blume, *Tetrastigma* Planchon, and members of the Icacinaceae). In recognition of its northern geography and the thermophilic affinities of many of its component taxa, Wolfe (1975, 1977) referred to this assemblage as the "boreotropical flora." The classic example of this flora is the Early Eocene London Clay assemblage of southeastern England (Reid & Chandler, 1933; Chandler, 1961, 1962, 1963, 1964, 1978). Although the boreotropical flora was apparently not a homogeneous unit, its composition was strikingly similar throughout its range. Reid and Chandler (1933) saw the modern Indomalaysian affinities of the London Clay assemblage as suggestive of a tropical flora that had moved along the coasts of the Tethys Seaway. This conclusion was subsequently supported by discovery of London Clay taxa in the Eocene of eastern Europe (Palamarev, 1973) and the Eocene (Chandler, 1954) and Oligocene (Bown *et al.,* 1982) of Egypt. The Middle Eocene Clarno Formation of Oregon represents an extension of this flora to the west (Scott, 1954; Chandler, 1964; Manchester, 1981, 1983), as do some small, unreported floras in the Rocky Mountains (pers. obs.).

Although the Clarno assemblage has not been fully investigated, it is clear that the fruit and seed portion of the flora includes several genera and perhaps some species in common with that of the London Clay. The geographic links between the Clarno and London Clay floras are conjectural; they could lie across the northern Pacific and East Asia (see data of Zaklinskaya, 1980), they could reflect the influence of the Tethys Seaway–North Atlantic route, or they could result from a combination of the two.

Once the early Tertiary boreotropical flora had spread, it was influenced and altered by subsequent geographic and climatic events, giving rise to the modern flora and vegetation of Eurasia and North America. Two geographic changes were of particular importance. In the Old World the closing of the Turgai Straits during the Oligocene (Vinogradov, 1967–1968; McKenna, 1975; see Map 5) permitted biotic exchange between central Asia and Europe. The disappearance of this sea also introduced a more continental climate to western Siberia. This led to the evolution of increasingly drought-tolerant, continental communities of a modern aspect, which ultimately invaded Europe from the east (see Friis, 1975). The second geographic modification involved the westward movement of North America. On its trailing edge this movement was powered by expansion along the Mid-Atlantic Ridge, which caused the widening of the North Atlantic and the sundering of early Tertiary ties between Europe and North America (McKenna, 1975, 1983a; Hoch, 1983). On its leading edge the westward movement contributed to the Tertiary orogenies of western North America. This mountain building provided direct topographic barriers to plant movement and resulted in a lengthening shadow of drier climates across central North America. Consequently, a new and more drought-tolerant flora and vegetation evolved in the western mountains and eastward, while the remnants of the earlier, moisture-adapted boreotropical flora were largely confined to the western slopes or retreated southward (Leopold & MacGinitie, 1972).

The effects of these geographic alterations were further modified by climatic changes through the Tertiary (Friis, 1975; Kennett, 1977; Buchardt, 1978; Wolfe, 1978; Hickey, 1981a). The temperate global climates of the earliest Tertiary gave way to increasingly warmer climates in the Early Eocene. During the latter time, much of the Northern Hemisphere supported a warm-temperate to subtropical vegetation, and thermophilic vegetation grew at fairly high latitudes (Wolfe, 1975, 1977). A climatic deterioration involving a decrease in world temperature and an increase in seasonality occurred during the later Eocene (Collinson et al., 1981; Keller, 1983) or at the Eocene-Oligocene boundary (Kennett, 1977; Buchardt, 1978; Wolfe, 1978) and extended into the Oligocene (Keller, 1983). This resulted in the contraction of the boreotropical flora and the geographic expansion of a species-poor deciduous vegetation of northern latitudes (Wolfe, 1969, 1977, 1978, 1980; Hickey, 1981a, 1981b, pers. comm.; Hickey et al., 1983). In the later Oligocene and the Miocene the climate fluctuated between warm and cool, leading to selection of cool-adapted taxa from the boreotropical flora and their addition to the developing deciduous vegetation, which diversified and is now recognized as the mixed mesophytic forest (Wolfe, 1969; see also Mai, 1964, 1981). Later Miocene and Pliocene

climates became increasingly cooler, leading to the extreme cold of the Pleistocene. This cooling resulted in a thermal segregation of the products of the boreotropical flora. The evergreen and cold-intolerant elements of the widespread Paleogene forests were restricted to protected southerly refugia; where these were not available, or where climatic change occurred more rapidly than dispersal and regeneration, local extinction occurred. The more recently segregated warm-temperate elements of the mixed mesophytic forests were likewise restricted to protected sites or became extinct, although the effects of glaciation were less disruptive on this group of plants than on the tropical members of the boreotropical flora. To the north a northern hardwood forest of low diversity developed, and north of it taiga and tundra communities evolved.

As a result of these geographic and climatic changes during the Tertiary, the evergreen and mixed mesophytic remnants of the boreotropical flora now occupy widely separated "Tertiary refugia." Classically, these include the Balkans, the Caucasus, Southeast Asia, Japan, western and eastern North America, and portions of the eastern highlands of Mexico (especially Veracruz) and northern Central America (see Szafer, 1964; Wood, 1972). Although these localities share common elements, they preserve different diversities and often different subsets of the boreotropical flora. Southeast Asia harbors the greatest representation of the early Tertiary flora, particularly in Japan and in the zone from the mixed mesophytic forests of China south through the tropical evergreen forests of Malaysia. The fossil record suggests that both western North America (Wolfe, 1975, 1977, 1978) and Europe (Chandler, 1964; Mai, 1964, 1970, 1981) had a rich sample of the boreotropical flora and the succeeding mixed mesophytic forest in the early and mid-Tertiary. However, the interaction of global climate and local topography caused the extinction of many of these thermophilic elements in the late Tertiary and Quaternary. This elimination was particularly pronounced in Europe, where advancing Pleistocene glaciers trapped the floras against the east–west oriented mountains, leaving only scraps of the original flora in Europe and more developed remnants in the diverse topography of the Balkans and the Caucasus. In western North America, boreotropical elements were first restricted to moister west-facing sites by the rising Rocky Mountains and were subsequently influenced by the cooling climates of the later Tertiary and Quaternary (Wolfe, 1969, 1977; Leopold & MacGinitie, 1972). Again, depauperization of the flora occurred, but with less drastic effects than in Europe.

Southeastern North America presently has a diverse representation of evergreen and deciduous woody elements of the boreotropical flora. The similarity of this flora to that of eastern Asia has been given as an example of disjunction since the time of Linnaeus (Graham, 1972) and Gray (1840, 1859; Boufford & Spongberg, 1983). However, the New World floras are generally considered to have a lower diversity of boreotropical elements than the modern floras of Japan, China, and Indomalaysia.

The contention that the modern descendant of the boreotropical flora in southeastern North America is less diverse than its counterpart in Southeast Asia is central to the discussion to follow. However, I do not believe this

statement has ever been supported in a quantitative manner, and I therefore present a numerical summary (TABLE). Hu (1935) estimated that there were 969 genera of woody spermatophytes and approximately 2000 species of trees in China. The second edition of the first five volumes of the *Iconographia Cormophytorum Sinicorum* (Anonymous, 1980) suggests a woody flora of approximately 950 genera and 3400 species. The *Iconographia* is acknowledged to be incomplete and is being superseded by the *Flora Reipublicae Popularis Sinicae*. This multi-volume flora is still being published and thus cannot be used to obtain a direct count of diversity. However, comparison of reports for 19 woody families in the *Iconographia* and the *Flora* suggests increases of roughly 15 percent in generic diversity and 100 percent in specific diversity in the latter publication. If this is correct, the woody flora of China would involve about 1030 genera and 6800 species. Ohwi's (1965) *Flora of Japan* records 278 genera and 858 species of woody spermatophytes from the much smaller area of Japan.

By contrast, *Gray's Manual of Botany* (Fernald, 1950) lists 161 genera and 665 species of woody spermatophytes (including trees, shrubs, and vines) in northeastern North America. The *Manual of the Vascular Flora of the Carolinas* (Radford et al., 1964) lists 211 genera and 554 species of woody spermatophytes in the flora of North and South Carolina. Small's (1933) *Manual of the Southeastern Flora* lists 412 genera and 1202 species of woody spermatophytes in the southeastern United States. Biases exist in all these tabulations, and the final figures must be taken as approximate. The *Iconographia Cormophytorum Sinicorum* embraces slightly more tropical areas than occur in the southeastern United States. The three North American sources cover separate portions of the flora of eastern North America rather than the entire flora (TABLE). Nonetheless, it is clear that the extant woody flora of eastern North America has approximately one-third to one-half the specific diversity of the woody flora of East Asia. While many of the East Asian genera are rare or monotypic, this is not the sole cause of the difference in diversity; comparison of vegetational surveys of China (Wang, 1961) and eastern North America (Braun, 1950) reveals 119 genera and 563 species of ecologically important trees in the former flora, and 46 genera and 112 species in the latter. Again, biases exist in the use of these data for the estimation of diversity, but the general picture is clear.

Herbs have not been mentioned in the above discussion inasmuch as a significant proportion of herbaceous taxa appear to have evolved locally in the middle and late Tertiary (Tiffney, 1981a, 1985) rather than spreading with the boreotropical flora. If they were included, it would only accentuate the observed pattern (see TABLE).

The cause of the lower diversity of boreotropical taxa in the modern flora of eastern North America is not immediately clear. Wolfe (1977) suggested four contributing factors: eastern North America was isolated from western North America and Europe in the Tertiary;[2] the Eocene-Oligocene climatic

[2]Wolfe (1977, p. 49) suggested, after MacGinitie (1969), that the isolation of eastern North America is ancient, and that the original Paleogene boreotropical flora of the area was less diverse than that of Europe or western North America.

Generic and Specific Diversities of Selected Eastern Asian and Eastern North American Floras.*

LOCATION	TOTAL AREA (sq. km)	TOTAL FLORA		WOODY PLANTS		HERBACEOUS PLANTS		PERCENT OF FLORA THAT IS WOODY	
		Genera	Species	Genera	Species	Genera	Species	Genera	Species
China a.	3,556,371	2389	7702	949	3397	1440	4305	40	44
b.		2840	15,400	1030	6790	1810	8610	36	44
Japan	369,698	988	3648	278	858	710	2790	28	23.5
N.E. North America	2,515,885	815	4227	161	665	654	3562	20	16
Carolinas	216,628	826	3157	211	554	615	2603	25.5	17.5
S.E. North America	1,700,374	1510	5563	412	1202	1098	4361	27	21.5

*All figures should be regarded as approximations. Introduced cultivated plants were excluded when identifiable as such. If a genus included more than one physiognomic type (e.g., tree, vine), placement of the genus and its included species in a physiognomic class was dictated by the prevalent physiognomy. In some cases this resulted in arbitrary decisions. The total number of taxa in a given area reflects both biological reality and the systematic concepts of the reporting author(s). For example, Small (1933) is generally regarded as a "splitter," and the absolute diversity reported in his flora is presumably inflated relative to the diversity reported by others. Sources: China "a," after Anonymous (1980); China "b," estimated from Anonymous (1959–present); Japan, Ohwi (1965); northeastern United States, Fernald (1950); the Carolinas, Radford *et al.* (1964); southeastern United States, Small (1933). Data for areas taken from Bartholomew *et al.* (1980); those for China exclude the floristically poor highlands of Tibet, Mongolia, and Sinkiang.

deterioration further depauperized the flora of eastern North America; this same event separated the incipient mixed-mesophytic flora of the area from more tropical floras isolated to the south, preventing enrichment of the former by the latter in the mid-Tertiary; and the area had little topographic diversity. Although the last point may be taken as given, the first three raise three sequential questions. First, was the Eocene boreotropical flora of eastern North America significantly less diverse than that of contemporaneous Europe or western North America? This involves both a consideration of the fossil record of eastern North America and an examination of the degree of geographic isolation of this area in the early Tertiary. Second, if this flora was as rich as that of Europe and western North America, did it give rise to an equally rich mixed-mesophytic flora, or as Wolfe has suggested, was its diversity curtailed by the Eocene-Oligocene climatic deterioration? Third, if diversity was not restricted by this deterioration, at what subsequent time was it reduced?

I believe that the original Paleogene boreotropical forest of eastern North America was nearly as rich as those of western North America and Asia, and that the reduced diversity of the present southeastern North American flora is a function of the subsequent Eocene-Oligocene and/or Pleistocene climatic fluctuations. Demonstration of this supposition is circumstantial and requires evidence from the fossil record and paleogeography. First, the Tertiary fossil record of eastern North America must be shown to contain a significant number of boreotropical taxa. The stratigraphic distribution of these taxa might aid in distinguishing between an Eocene-Oligocene and a Pleistocene depauperization of the flora. Second, examination of the paleozoogeography, paleogeography, and paleoclimatology of the early Tertiary must demonstrate that eastern North America was not isolated from the rest of the Northern Hemisphere during the spread of the boreotropical flora. I will examine these two lines of evidence and suggest that the data, although equivocal, support the contention of a diverse early Tertiary flora in eastern North America that was reduced by subsequent, primarily climatic changes.

THE PALEOBOTANICAL RECORD OF EASTERN NORTH AMERICA

Our present understanding of the Tertiary paleobotanical history of eastern North America is poor. Paleogene and Neogene plant-bearing deposits are rare on the Atlantic Coastal Plain. The tectonic setting of this area in the Tertiary did not favor the formation of deep depositional basins. The few fossiliferous deposits that accumulated have been severely eroded by ice sheets in glaciated terrain and deeply weathered to the south of the limit of glaciation. The low angle of repose of the present terrain does not favor natural exposure of the coastal plain sediments, and extant vegetation hampers exploration efforts. Finally, few workers are investigating this time and area.

In spite of these difficulties, evidence for the presence of boreotropical genera may be found in both the micro- and the macrofossil records. Among microfossils, Elsik (1974) has recorded pollen of *Engelhardtia* Leschen. ex Blume, *Pterocarya* Kunth, *Platycarya* Sieb. & Zucc., *Alangium* Lam., *Ficus* L., and the Icacinaceae, and Frederiksen (1980b) reported pollen of the palm *Nypa*

from Middle and Upper Eocene sediments of the Mississippi Embayment. The pollen of *Platycarya* is of particular note since it peaks both in the Early Eocene floras of the Atlantic Coastal Plain and the Mississippi Embayment (Frederiksen, 1980c) and in the Early Eocene Willwood Flora of Wyoming (Wing, 1981). Although circumstantial, this implies a degree of Early Eocene floristic exchange between the southeast and the eastern slope of the Rocky Mountains. Traverse (1955) recorded pollen of *Engelhardtia, Pterocarya, Alangium,* and *Glyptostrobus* Endl. from the Brandon Lignite of Vermont. This deposit has been dated as Oligocene (Wolfe & Barghoorn, 1960) or perhaps Early Miocene (D. Mai, pers. comm.; N. Frederiksen, pers. comm.) in age. Frederiksen (1984) has found pollen of *Sciadopitys* Sieb. & Zucc., *Pterocarya,* and the *Engelhardtia* "group" (*Engelhardtia, Alfaroa* Standley, *Oreomunnea* Oersted) in the Miocene of Massachusetts, and Rachele (1976) has recorded pollen of *Pterocarya* and *Engelhardtia* in the Miocene of New Jersey. All of these genera are members of the boreotropical flora and currently exist in the flora of East Asia. However, although present in the Tertiary pollen floras of eastern North America, these taxa formed a small percentage of the total flora; in most cases the pollen floras of this area appear to be dominated by New World taxa or by pollen taxa that lack specific biogeographic affinities.

The macrofossil record of the Gulf Coastal Plain is poor for the late Tertiary but far better for the Paleogene. Revisions of Berry's (1916, 1924, 1930) early studies on the leaves of the Mississippi Embayment deposits have only recently been initiated (Dilcher, 1971; Crepet, 1979, and references therein), and comparison of these leaf floras with others in the Northern Hemisphere is difficult. The existing data suggest some similarity between the floras of the Embayment and those of the early Tertiary of western North America (Wing, 1981). However, the degree of this similarity is not fully understood, and the timing of its onset or decline is unclear. Climatic reconstructions using leaves (Dilcher, 1973) and pollen (Frederiksen, 1980a) suggest that the warm climates of the earlier Eocene in the Northern Hemisphere were distinguished in the southeast by a pronounced dry season. If this is correct, such a seasonal drought may have promoted the evolution of a flora and vegetation distinct to some degree from that of western and northeastern North America. The one megafossil from the Mississippi Embayment with a clear boreotropical affinity is the fruit of the palm *Nypa* from the Middle Eocene of Texas (Arnold, 1952; Tralau, 1964), which is also known from pollen (Frederiksen, 1980b). *Nypa* was widely distributed in the early Tertiary of Europe (Tralau, 1964) but is presently restricted to estuarine sites in Indomalaysia and northern Australia.

Outside of the Mississippi Embayment, macrofossils have been studied less frequently than microfossils, yet they often provide more specific biogeographic information. The fossil distribution of *Nypa* is paralleled by that of two species of ?Euphorbiaceae from the Early Eocene of Maryland and Virginia, *Wetherellia* Reid & Chandler and *Palaeowetherellia* Chandler (Mazer & Tiffney, 1982). *Wetherellia* is known from Eocene sediments in England (Reid & Chandler, 1933; Chandler, 1964) and is one of the most common elements of the London Clay; *Palaeowetherellia* is known from early Tertiary deposits in northern Egypt (Chandler, 1954). Although specimens of the latter genus from Egypt and the

New World are clearly different from one another, those of *Wetherellia* from England and the Atlantic Coastal Plain are virtually indistinguishable, and their depositional context suggests that they were produced by a coastal plant. The distributions of these two taxa, and of *Nypa,* appear to reflect the westerly extension of coastal elements of the London Clay Flora along the northern shore of the Tethys.

The one exception to the dearth of macrofossil deposits in northeastern North America is the Brandon Lignite of west-central Vermont. This deposit is rich in pollen, wood, fruits, and seeds; its age is uncertain but probably falls between Oligocene (Wolfe & Barghoorn, 1960) and Miocene (Frederiksen, pers. comm.). The flora is pertinent to the present discussion because it provides an instructive comparison between the biogeographic information inherent in micro- and macrofossil floras, and because it demonstrates the presence of several boreotropical genera in the Tertiary of eastern North America that are not found in the extant flora of this area. The only boreotropical genera recorded in the microflora (Traverse, 1955) are *Alangium, Engelhardtia, Glyptostrobus,* and *Pterocarya*; the remainder of the palynoflora appears to have New World or cosmopolitan affinities. By contrast, the macroflora includes both some taxa with close relationships to modern genera restricted to East Asia, and a smaller number of taxa related to boreotropical forms found in the Tertiary floras of Europe. *Nyssa brandoniana* Eyde & Barghoorn (Eyde & Barghoorn, 1963) is very similar to *N. javanica* (Blume) Wangerin of Burma. *Phellodendron* Rupr. and *Euodia* J. R. & G. Forster (Rutaceae; Tiffney, 1980a) are presently restricted to East Asia but were common in Europe during the Tertiary. *Turpinia* Vent. (Staphyleaceae; Tiffney, 1979) is found in both the Old and New World tropics. The Brandon specimen shows closer affinity with existing New World species; a second species is found in the European Miocene (Mai, 1964). Similarly, *Cleyera* Thunb. (Theaceae; Tiffney, in manuscript) is largely a New World genus but is closely related to the Old World *Eurya* Thunb. *Cleyera/Eurya*-like fossils are common in the European Tertiary, and the two genera are probably sister groups of Tertiary origin. *Magnolia waltonii* Tiffney (Magnoliaceae; Tiffney, 1977) and *Microdiptera parva* Chandler (Lythraceae; Tiffney, 1981b) are both Brandon taxa that are closest to extinct forms of the European Tertiary. Undescribed fossils now under investigation include achenes similar to those of *Caldesia* Parl. (Alismataceae), a genus of the Old World tropics and known from the European Tertiary, and at least three species of *Symplocos* Jacq., only one of which appears to have New World affinities. In addition, endocarps of *Alangium* (Alangiaceae; Eyde *et al.,* 1969), paralleling the pollen record, are known from the deposit.

Although the fruit and seed flora of the Brandon Lignite has not been fully described, it does include several clearly boreotropical taxa and is far more closely related to the boreotropical flora than would have been judged from the associated microflora. Further, this flora is later than Eocene in age and emanates from a very small deposit (only a few cubic yards of fossiliferous sediment are available for study). These last two factors suggest that the Brandon Flora is probably a limited subset of the boreotropical flora that was originally in eastern North America.

In summary, palynological evidence suggests that a few boreotropical taxa now restricted to eastern Asia were present in the earlier Tertiary of eastern North America. However, compared to western North America (e.g., Leopold & MacGinitie, 1972), eastern North America appears to lack several common boreotropical pollen taxa in the early Tertiary. By contrast, macrofossil evidence from two isolated occurrences of fruits and seeds, and from the Oligocene or Miocene Brandon Lignite, demonstrates the presence of boreotropical elements in eastern North America. The assemblage of boreotropical taxa in the Brandon Lignite indicates that eastern North America had a greater initial diversity of boreotropical taxa—and perhaps of derived mixed mesophytic taxa—than has previously been suspected. The paleofloristic affinities of the Paleogene floras of the Mississippi Embayment are presently unclear, although limited evidence suggests some floristic interchange with western North America in the early Tertiary. The fossil record is too scanty to resolve the timing of the depauperization of the eastern North American flora.

PALEOGEOGRAPHIC EVIDENCE ON THE DEVELOPMENT OF THE EASTERN NORTH AMERICAN FLORA AND VEGETATION

If eastern North America was separated from other northern continents in the early Tertiary, this would reinforce Wolfe's (1977) suggestion that the lower current diversity of the southeastern North American flora stemmed from its early isolation from the general boreotropical flora. However, if early Tertiary connections with other portions of the Northern Hemisphere can be demonstrated, this would support the contention that the lower current diversity is a function of later Tertiary events and would parallel the fossil data enumerated above.

The connection of eastern North America to other boreal landmasses is bidirectional. The classic perception (e.g., H. L. Li, 1972), perhaps influenced by the present proximity of Siberia and Alaska, suggests a linkage through western North America. This route involves two subunits: the connection of eastern Asia to western North America across the Bering Straits, and that of western to eastern North America through the mid-continental area. The alternative route involves linkage of eastern North America to Europe across the early Tertiary North Atlantic. Although accepted by paleozoologists (e.g., Lehmann, 1973; McKenna, 1975, 1983a; Russell, 1975), the latter route is rarely considered by paleobotanists; only Tiffney (1980b) and Wolfe (manuscript submitted) have discussed its significance in early Tertiary phytogeography. This route is also bipartite, involving the linking of North America to Europe, and of Europe to East Asia. Each of these routes of connection will be considered.

THE BERING CONNECTION

The Bering land bridge has been recognized in biogeographic discussions for nearly a century (e.g., Matthew, 1915; Hopkins, 1967). The vertebrate paleontological record of Beringia suggests a barrier to faunistic exchange in

the Paleocene (Chow & Zheng, 1979), an Early Eocene period of connection between Alaska and Siberia, a Middle Eocene period of isolation, and a limited Late Eocene resumption of exchange (Kurtén, 1966; Novodvorskaja & Janovskaja, 1975). The nature of the barrier to exchange is not certain; it could involve climate and/or land position. Kurtén noted that the Early Eocene exchange between eastern Asia and western North America involved elements different than those found in Europe and North America at the same time.

During the Eocene, world climates (Kennett, 1977; Buchardt, 1978; Wolfe, 1978; Collinson et al., 1981; G. Keller, 1983) were warm enough to support thermophilic vegetation and vertebrates (e.g., Estes & Hutchison, 1980; McKenna, 1980) at far northern latitudes. The primary limitation to the northerly extent of evergreen boreotropical taxa at this time was light (Allard, 1948; Hickey, pers. comm.).

In earlier papers Wolfe (1972, 1977) suggested the presence of evergreen forms in Alaska north of their modern latitudinal limit of tolerance to low light levels. On this basis he postulated (Wolfe, 1975) that the angle of inclination of the earth's axis of rotation was lower during the Eocene. This suggestion has drawn much criticism (e.g., Donn, 1982; McKenna, 1983b), and theoretical models of climate (Eric Barron, pers. comm.) suggest that such a change would actually lead to polar paleotemperatures much colder than those inferred. More recently, Wolfe (manuscript submitted) has reevaluated the distribution of floras in northwestern North America and has concluded that the Eocene Bering land bridge was primarily occupied by a broad-leaved, deciduous forest, perhaps with a thin southern fringe of evergreen, megathermal communities. As a result, Wolfe suggests that the Bering bridge is of limited importance in explaining the spread of megathermal elements of the Eocene boreotropical flora.

Estimation of the degree of floristic movement of evergreen taxa across the Bering bridge is complicated by the complex tectonic history of this area. Alaska lay somewhat north and east of its present position in the early Tertiary (Smith & Briden, 1977), but its southern margin was in flux. Much of Pacific North America is now considered to be formed of an aggregation of "microplates" that have drifted against North America. Many of Wolfe's Paleogene floras are located on these terranes (see MAP 1). The exact paths of movement and times of collision of these plates with western North America are the subject of debate and active research. The literature (e.g., Coney et al., 1980; Ben-Avraham et al., 1981) generally suggests that accretion was over by the early Tertiary, but recent evidence (Cowan, 1982; Bruns, 1983) demonstrates that some terranes may have moved considerable distances as recently as the mid-Tertiary. It appears that most of these plates collided with North America at about the latitude of British Columbia and then slid northwestward toward Alaska. If so, these terranes had little impact on the phytogeography of the Bering bridge. However, it is not clear at this time that this is true for all these terranes. For the present, phytogeographers should continue to consider the possibility that some of these terranes may have formed island "stepping stones" south of Alaska in the early Tertiary, perhaps connecting to Asia via islands associated with the ancestral Aleutian arc (DeLong et al., 1978). However, this geographic
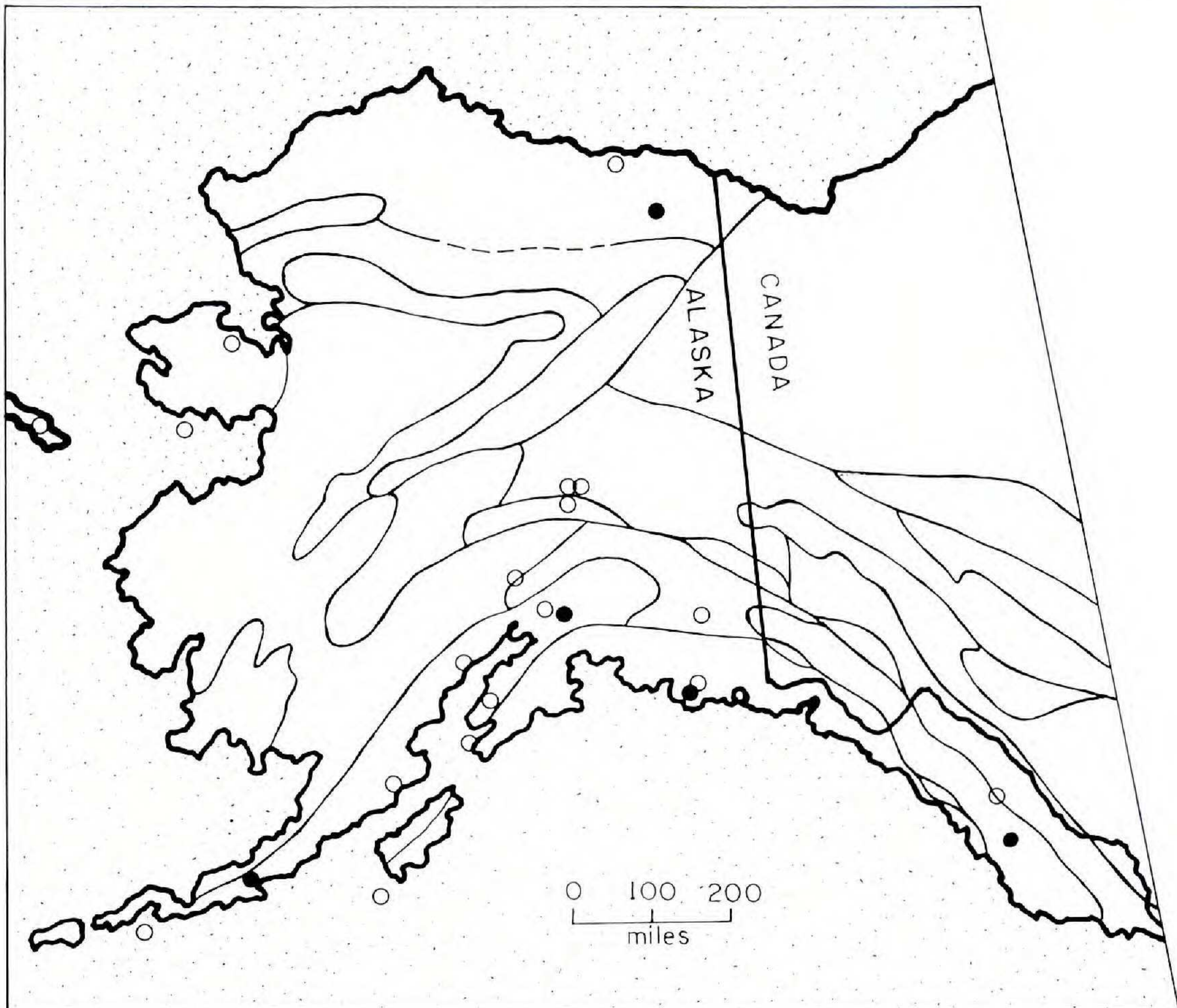
Map 1. Alaska, combining margins of presently identified allochthonous terranes (after Ben-Avraham *et al.*, 1981, *fig. 7*) with Tertiary floras reported by Wolfe (1972) from this area. Light lines = terrane margins, closed circles = Paleocene and Eocene floras, open circles = Oligocene or later floras. All Paleogene floras except Sagavanirktok on north slope lie on recently accreted terranes.

arrangement is highly tentative, and the limited available habitat of such an island chain would curtail its biogeographic significance (McKenna, 1983b).

I conclude that the Bering land bridge was a viable route for the exchange of deciduous boreotropical taxa in the early Tertiary. Evergreen elements of this flora were probably restricted in their use of the Bering bridge by day length. Alternative, more southerly routes were limited in area, if they existed. The climatic deterioration of the later Tertiary (Kennett, 1977; Buchardt, 1978; G. Keller, 1983) increasingly restricted this route to cool-temperate taxa.

The Central North American Problem

Floristic exchange between western and eastern North America involves the central portion of the continent, but evidence is inferential about the degree to which this could or did occur. The terrestrial plant record of this area is limited to a few primarily Neogene localities (e.g., MacGinitie, 1962; Segal, 1966a, 1966b; Thomasson, 1977, 1980a, 1980b), with the exception of the
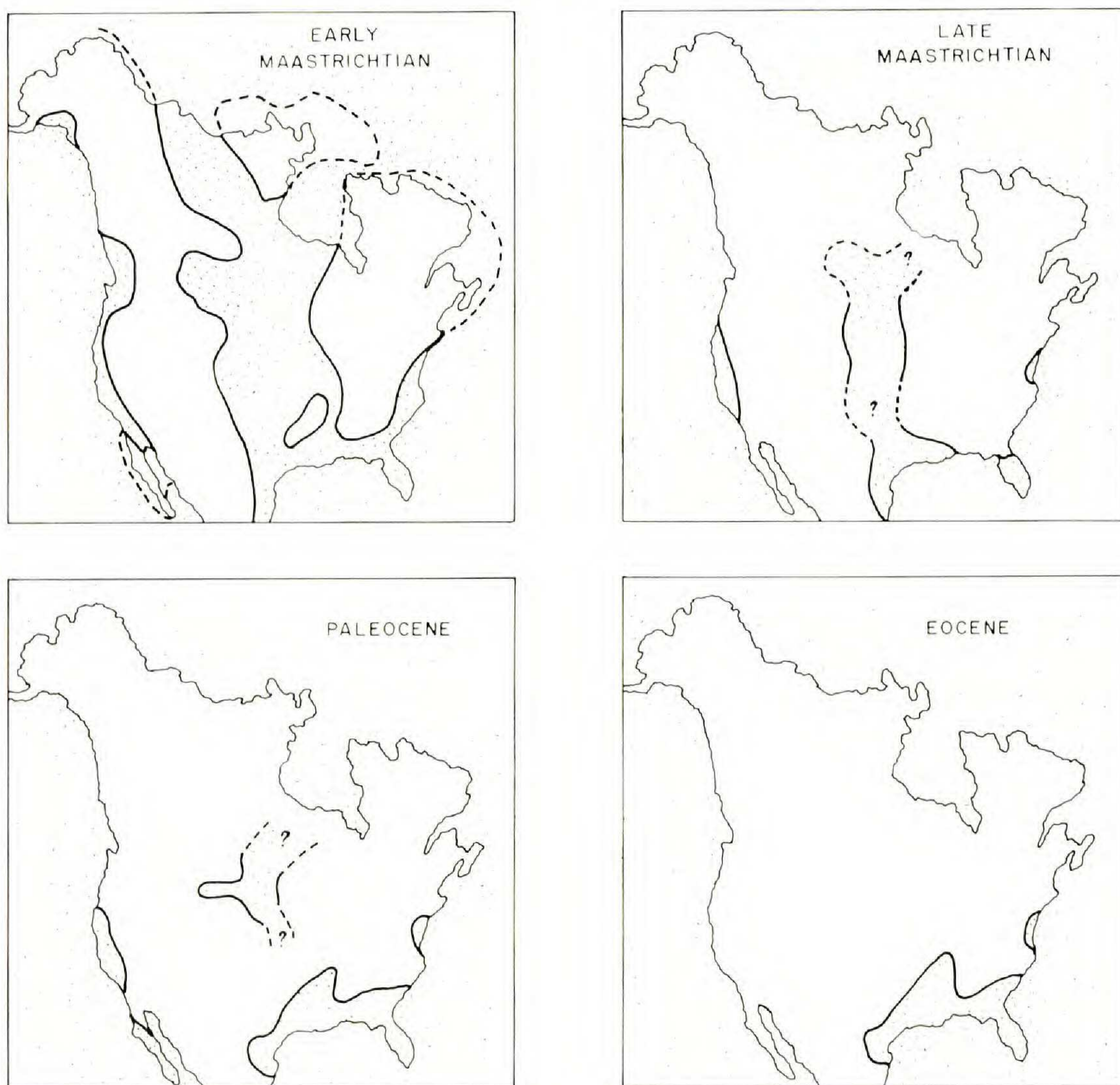
MAP 2. Sequential generalized paleogeography, Late Cretaceous to early Tertiary, showing regression of North American Mid-Continental Seaway (shaded area). Data after Schuchert (1955), Reeside (1957), Gill and Cobban (1966), McDonald (1972), McGookey *et al.* (1972), and Williams and Stelck (1975).

Late Paleocene–Early Eocene Golden Valley Flora of North Dakota (Hickey, 1977).

Central North America was occupied by an epicontinental seaway in the Late Cretaceous. This formed a relatively successful phytogeographic barrier, separating the largely western North American *Aquilapollenites* floristic province from the largely eastern North American–European normapolles province (Muller, 1970). This seaway retreated to the north and south in the latest Cretaceous and Paleocene (MAP 2), eliminating its moderating climatic influence and giving way to an increasingly continental climate. This regression occurred concomitantly with the uplift of the Rocky Mountains, which as they rose, cast an increasingly long rain shadow to their east (Leopold & MacGinitie, 1972). The temporal relationship between the spread of the boreotropical flora, the retreat of the seaway, and the development of these drier climates is unclear. In particular, the exact geographic borders of the Late Cretaceous Mid-Con-

tinental Seaway and of the Paleocene Cannonball Sea have not been rigorously demonstrated in the geologic literature. Late Paleocene–Early Eocene floras from the eastern face of the present Rocky Mountains (e.g., Hickey, 1977; Wing, 1981) contain a few boreotropical elements, as well as some elements in common with the Eocene of the Mississippi Embayment (Wing, 1981). Wolfe (manuscript submitted) suggests that Wing's and Hickey's floras may have been dominated by floodplain vegetation, and that the interfluvial areas may have supported a paratropical rainforest. Leopold and MacGinitie (1972) noted that the Early Eocene floras of the Rocky Mountain region have East Asian affinities, while those of the Middle Eocene are dominated by taxa with relatives in the New World tropics. They associated this change with increasing seasonality of rainfall from the Early to Middle Eocene, presumably related to the uplift of the Rocky Mountains. This suggests that a moisture-based filter-barrier came into existence between eastern and western North America by the Middle Eocene. However, the barrier may not have been continuous; corridors of migration may have existed along rivers flowing eastward from the mountains to the plains. Perhaps the most tantalizing evidence for the later Paleogene plant communities of central North America comes from Retallack's (1983a, 1983b) investigations of fossil soils in South Dakota. These suggest that forest communities were in this area in the Late Eocene and Early Oligocene, but that they gave way first to savannas and then grasslands in the later Oligocene. This raises the possibility that a corridor of forest existed across the central-northern plains in the early Tertiary, perhaps invading drier areas along river courses. However, no evidence exists as to the composition of this forest or as to its extent beyond South Dakota. Some boreotropical elements are found in the Miocene Kilgore Flora of Nebraska (MacGinitie, 1962), but these are generally of cool-temperate affinity and have limited relations with the modern flora of East Asia. No evidence exists for the nature of Tertiary floras in the glaciated portions of Canada; it is possible that forest could have stretched across the higher latitudes of central North America in the early Tertiary.

In summary, evidence for the potential and actual movement of elements of the boreotropical flora across mid-continental North America is scanty. Logic suggests that climatic changes attendant upon the retreat of first the Mid-Continental Seaway and then the Cannonball Sea, together with the rise of the Rocky Mountains, would have created a filter to the movement of moisture-loving plants. However, the timing of these events, and the nature of mid-continental climates and floras in the Paleocene and Eocene, are unknown. Further, scattered fossil evidence suggests that some elements of the boreotropical flora (e.g., *Platycarya*) did move through this area. Evidence from fossil soils suggests that closed forest may have existed in the central plains until the Early Oligocene. The Middle Eocene Clarno Flora of Oregon contains several presumably evergreen boreotropical elements (Manchester, 1981); if these did not reach the west coast of North America by way of the Bering bridge (see data of Wolfe, in press), then they must have achieved their distribution via central North America. As long as evidence for the early to middle Tertiary environments of the Great Plains is unclear, the potential importance of this area as a migration route of the boreotropical flora remains moot.

THE EUROPEAN–EASTERN NORTH AMERICAN CONNECTION

A paleofloristic link between Europe and eastern North America has been viewed as "possible" by many authors (e.g., Graham, 1964; Raven & Axelrod, 1974; Wolfe, 1975, 1977). In general, it has never been given the importance of the Beringian connection, although I suggested it earlier (Tiffney, 1980b), and Wolfe (manuscript submitted) has recently concluded that it was probably more important than the Bering bridge. A similar opinion has been held by some paleozoologists (see McKenna, 1975), who originally claimed that the Eocene faunal similarity of North America and Europe was attained by a trans-Asiatic migration route. Recent evidence, both geologic and paleontological, has suggested that this is incorrect, and McKenna (1972, 1975, 1983a) has cogently argued for the importance of North Atlantic land connections in explaining the distribution of early Tertiary vertebrates. Similarly, I believe that the North Atlantic connection has played a major part in the spread of the boreotropical flora and in the development of the similarity of the East Asian and eastern North American floras. Consideration of the North Atlantic connection will be on three levels: geologic, paleozoological, and botanical.

GEOLOGIC DATA. The potential of a North Atlantic land bridge has been recognized since Wegener's original suggestion of continental drift, but only within the last decade has definite evidence for this bridge been produced. A land link between Europe and America involves two stages: Europe to Greenland and Greenland to North America. It is appropriate to consider each separately.

The geologic evidence for a Europe-Greenland connection is excellent and has been exhaustively reviewed by McKenna (1983a), from which much of the following summary is drawn, and to which the reader is referred for references and details. McKenna recognizes two geographically and temporally separate links between Greenland and Europe: a northerly "DeGeer" route from northern Scandinavia to northern Greenland, and a southern "Thulean" route from northern Scotland through the Faeroes and Iceland to southern Greenland (MAP 3). The DeGeer route is of somewhat less interest to a discussion of the boreotropical flora for two reasons. First, it lay ten to fifteen degrees higher in latitude than the Thulean route, although it was still at a lower paleolatitude than the coeval Beringian bridge situated at almost 75°N latitude (McKenna, 1972). Second, the DeGeer route terminated in northern Scandinavia, which according to McKenna (1983a), was separated from direct contact with Europe for much of the Paleogene by the Danish-Polish trough and its southerly extension, the "Moravian portal," linking the trough to the Tethys (Pożaryska & Cuik (1976), Pożaryska (1978); see McKenna (1983a) for discussion). However, there is not agreement on the presence of this sea barrier throughout the Eocene. Plaziat (1981, *figs. 21, 22*; 1983, *fig. 5*) suggested that southwestern Europe was isolated from Fennoscandia in the Paleocene, but that the responsible seaway retreated by the Early Eocene, reconnecting the two land masses. I follow McKenna (1983a) in showing a marine barrier between southwestern Europe and Fennoscandia in MAPS 3, 4, and 6, but this is a moot point. Similarly, the Turgai Straits isolated Fennoscandia from eastern Asia for much of the Paleogene (Hoch, 1983; McKenna, 1983a). The DeGeer route was prob-
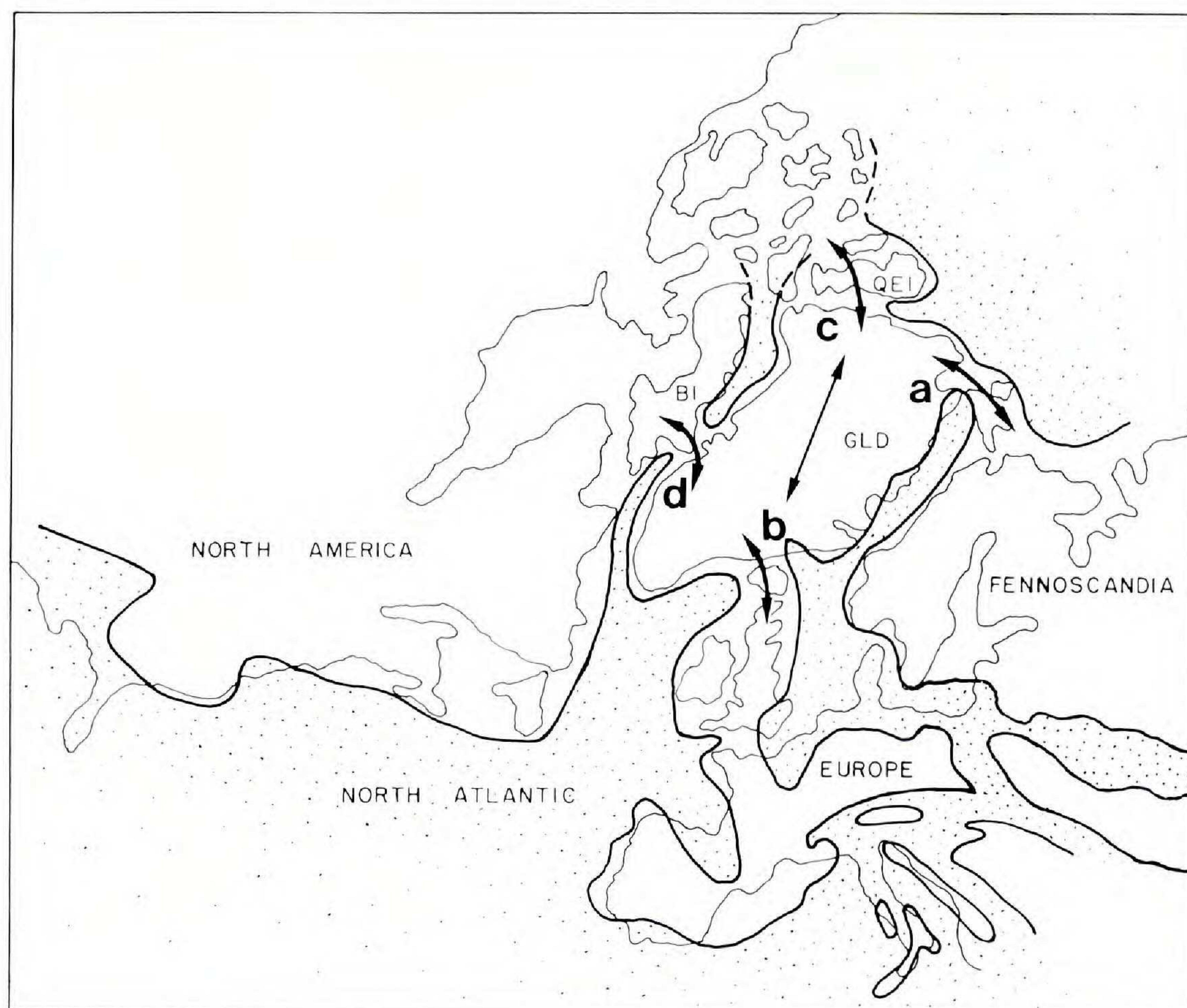
MAP 3. Generalized paleogeography of North Atlantic area in Early Eocene, showing possible routes of connection between Europe and North America. Connection "a" = McKenna's DeGeer route linking Fennoscandia and northern Greenland (GLD); "b" = McKenna's Thulean route from southwestern Europe to southern Greenland; "c" links northern Greenland to Queen Elisabeth Islands (QEI); "d" = potential link between central Greenland and Baffin Island (BI). Dispersal may have occurred in either direction over any bridge (heavy arrows); dispersal within Greenland (light arrow) may have resulted in several entry/exit route patterns. Shaded area = sea; heavy lines = paleo-coastlines; light lines = present coastlines. Assembled from, but not necessarily adhering to, McKenna (1972, 1983a, 1983b, pers. comm.), Pożaryska (1978), Heissig (1979), Buchardt (1981), Srivastava et al. (1981), and Pomerol (1982).

ably present as early as the Danian, although the climate of that time (Buchardt, 1978; Wolfe, 1978; Hickey, 1981a) suggests that it would be restricted to cold-tolerant organisms. This route functioned through the latest Eocene or Early Oligocene, when it was terminated by the linkage of the Greenland-Norwegian Sea and the Arctic Ocean. During the Early Eocene, warm climates may have made it passable to thermophilic biota, but the effect of winter day-length is uncertain. The Early Eocene flora from Ellesmere Island (Hickey et al., 1983; Hickey, pers. comm.) appears to include only deciduous angiosperms in conjunction with a thermophilic fauna (Estes & Hutchison, 1980). This suggests that winter day-length was the limiting factor.

The initiation of active sea-floor spreading northwest of the British Isles in

the Late Paleocene resulted in the first appearance of the Thulean bridge. Again, the cool climates of the time restricted biotic access to this route. However, the succeeding Early Eocene was a time of widespread warm climates (Wolfe, 1978; Buchardt, 1978; Collinson *et al.*, 1981), which opened the Thulean route to passage by warm-adapted organisms. Further, since this route lay between 45° and 50°N paleolatitude, winter sunlight would have been sufficient to permit the passage of evergreen taxa (MAP 3). Most evidence suggests that this connection was suddenly broken in the Early Eocene (McKenna, 1983a) or latest Paleocene (Hanisch, 1983) and was never reestablished (but see Grønlie (1979), who suggested that it may have persisted piecemeal until the mid-Miocene, and Strauch (1970, 1972), who suggested that a fairly substantial land bridge existed throughout most of the Tertiary).

The linkage between Greenland and northeastern North America across the Davis Strait is the subject of considerably more debate (e.g., Dawes & Kerr, 1982). The Davis Strait, and its extension through Baffin Bay and the Kane Basin, apparently linked the Atlantic and Arctic oceans in the latest Cretaceous and Early Paleocene. Invertebrate fossils suggest that a bridge between Greenland and the Queen Elisabeth Islands may have come into being in the Danian and have continued through much of the Eocene. Circumstantial evidence (e.g., terrestrial sediments beneath the Davis Straits (McKenna, 1983a, and pers. comm.)) exists for a land connection to the south between Greenland and Baffin Island, but the assembled data (McKenna, 1983a) are not as conclusive. The northern bridge falls at nearly the same latitude as the DeGeer route; thus, winter day-length might restrict its importance to deciduous angiosperms and conifers. The southern route is at a substantially lower latitude and would have permitted passage of evergreen taxa.

In summary, the geologic evidence suggests a clear northern connection from Scandinavia to northern Greenland and from northern Greenland to the Queen Elisabeth Islands from Late Paleocene to Late Eocene (MAP 3). A second connection from the British Isles to southern Greenland existed briefly in the Late Paleocene and Early Eocene. This probably was matched by a lower-latitude bridge from central Greenland to Baffin Island and northeastern Canada at the same time, although the geologic evidence is not clear. Certainly southwestern Europe was in connection with North America via the Thulean bridge on the east and the northern Greenland–Queen Elisabeth Islands bridge on the west during a brief portion of the Early Eocene.

PALEOZOOLOGICAL DATA. Vertebrate paleontology supports the existence of a European–North American connection. The similarity of the Early Eocene faunas of North America and Europe was recognized by earlier workers (see McKenna, 1975, for a summary and a list of taxa in common). The degree of correspondence of the two faunas began to rise in the Late Paleocene, peaked in the Early Eocene when roughly 60 percent of the known European genera were held in common with North America (Lehmann, 1973), and then declined precipitously by the Middle Eocene. The decline in faunistic similarity probably lagged behind the actual geographic isolation, as biologic differentiation of the isolated populations took time. The rise and fall of this similarity parallels the

projected appearance and demise of the Thulean route. Data concerning the early Tertiary vertebrate paleontology of Greenland are presently lacking (Hoch, 1983; McKenna, 1983a), curtailing a more exact description of the exchange.

BOTANICAL DATA. Paleobotanical and botanical data regarding the Atlantic bridge are less common than paleozoological data. However, in the context of the geologic and vertebrate paleontological information given above, I believe that a convincing, if inferential, case can be made for passage of the boreotropical flora across the Atlantic bridge. Four lines of botanical data are considered. First, several fossil taxa of eastern North America are specifically similar to fossils known from the Tertiary of Europe. *Nypa* (Arnold, 1952; Tralau, 1964) and *Wetherellia* (Mazer & Tiffney, 1982) are classic European early Tertiary taxa, and the New World species are virtually identical to their Old World counterparts. Similarly, *Microdiptera parva* from Brandon (Tiffney, 1981b) has previously been described only from Europe and western Siberia. Second, several genera from the Brandon Lignite (*Phellodendron, Euodia, Turpinia, Alangium,* and *Symplocos*) are thermophilic elements that were also common in the European Paleogene. *Symplocos* provides a particular example of this pattern, because the genus is very diverse in the European Tertiary (Mai, 1970) and is disproportionately represented in the Brandon Flora by at least three species. Third, several modern taxa known as fossils in the European Tertiary presently survive only in eastern North America. Among flowering plants these include *Asimina* Adanson (Annonaceae), *Calycocarpum* Nutt. ex Torrey & Gray (Menispermaceae), *Comptonia* L'Hér. ex Aiton (Myricaceae), *Decodon* J. F. Gmelin (Lythraceae), *Dulichium* Pers. (Cyperaceae), *Fothergilla* L. (Hamamelidaceae), *Leitneria* Chapman (Leitneriaceae), *Polanisia* Raf. (Cleomaceae), *Proserpinaca* L. (Haloragidaceae), *Ptelea* L. (Rutaceae), *Robinia* L. (Leguminosae), and *Sabal* Adanson and *Serenoa* Hooker f. (Palmae). An interesting parallel is provided by the hickory aphid (*Longistigma caryae* Harris), which is presently restricted to North America but is reported from Upper Miocene–Lower Pliocene sediments in Iceland (Heie & Friedrich, 1971). An additional group of taxa is common to the extant floras of Europe and North America. Although many of these taxa attained this range in the later Tertiary or Quaternary (see Löve & Löve, 1963, for a general discussion of late and post-Tertiary links between Europe and North America), many others (e.g., *Fagus* L., *Juglans,* or the gasteromycete *Lycoperdon* Tourn.; see Demoulin, 1973) appear to represent remnants of generally dispersed boreotropical taxa. Fourth, as discussed above, several boreotropical taxa are known as fossils from eastern North America. If the Bering bridge is less important as a North American access route for evergreen boreotropical taxa (see Wolfe, manuscript submitted), then these taxa presumably came and went from North America via the North Atlantic bridge. In summary, the plant evidence is scattered and circumstantial. Taken alone, any of the above examples is weak since it is never clear where a single taxon may have occurred in the past in addition to those places from which it is presently known as a fossil. However, in its entirety, the plant evidence does not contradict the existence of a North Atlantic bridge and appears to support it.
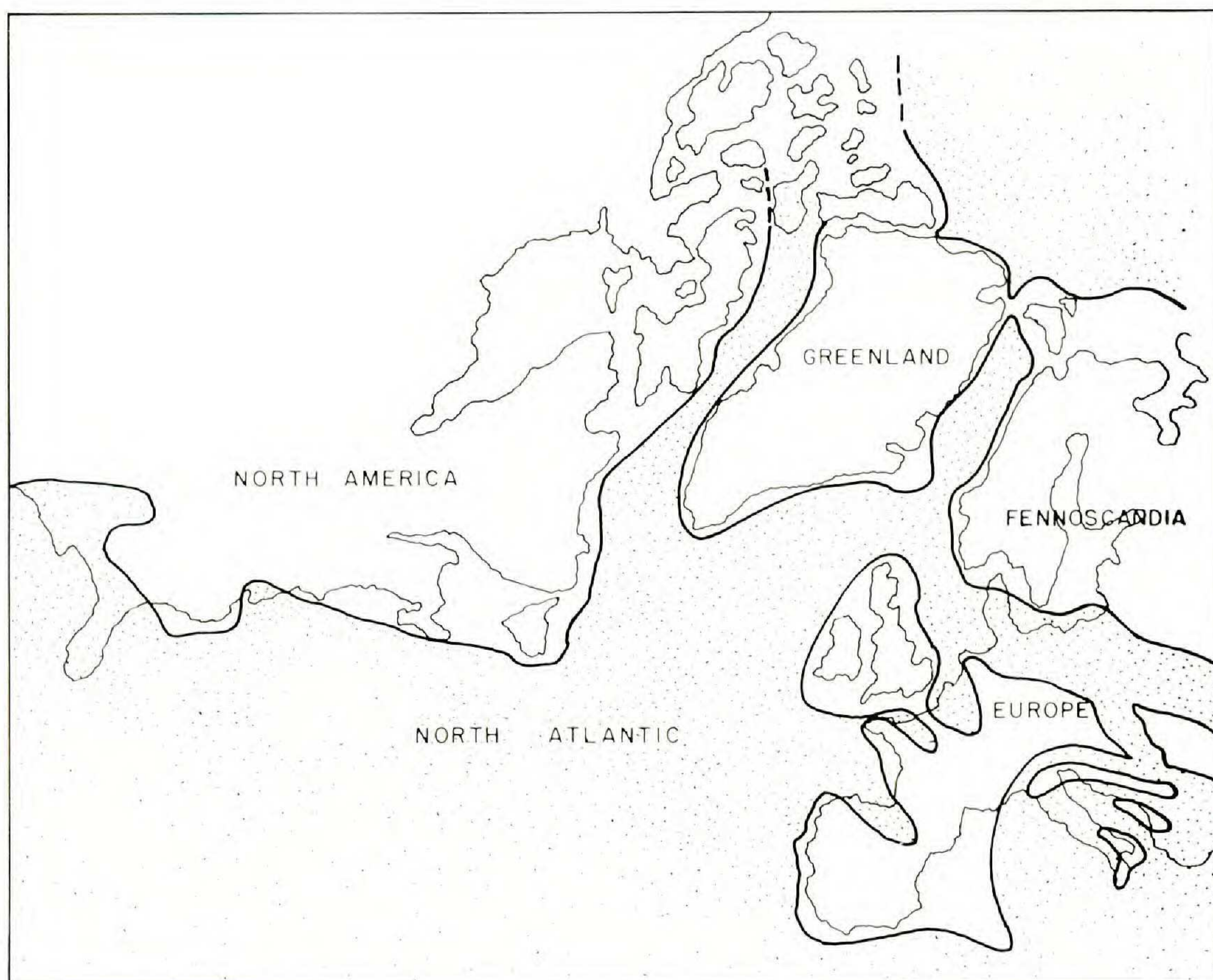
MAP 4. Generalized paleogeography of North Atlantic area in Late Eocene, showing changes in land continuity following spreading in Greenland-Norwegian Sea and Davis Straits between Greenland and Baffin Island. Connections between Queen Elisabeth Islands and Greenland, and Greenland and northern Europe, probably existed but were likely closed to thermophilic organisms by Late Eocene climatic decline. Conventions and sources as in MAP 3.

In conclusion, geologic data indicate the presence of two Early Eocene bridges between Greenland and Europe (one to Fennoscandia and one to southwestern Europe), and two Early Eocene land bridges from Greenland to North America (one via the Queen Elisabeth Islands, and a less well defined one from Greenland to Baffin Island) (MAP 3). Evidence from vertebrate paleontology suggests that these routes were used by terrestrial and freshwater vertebrates. Flowering plants must also have passed across these same bridges, but evidence of their nature (deciduous or evergreen; cool tolerant or intolerant) is not directly available. However, it is unlikely that the vertebrates common to Europe and North America would have strayed far from familiar vegetational environments or food sources. For this reason, it can be assumed that the vertebrates migrated across the North Atlantic land bridge in conjunction with the boreotropical flora. Further, a significant proportion of this fauna was herbivorous or omnivorous (McKenna, 1975), and such animals would be expected to disperse their food plants. Thus, while the individual elements of evidence do not clearly indicate passage of the boreotropical flora across the Early Eocene North Atlantic land bridge, the sum of information argues strongly that this was the case.
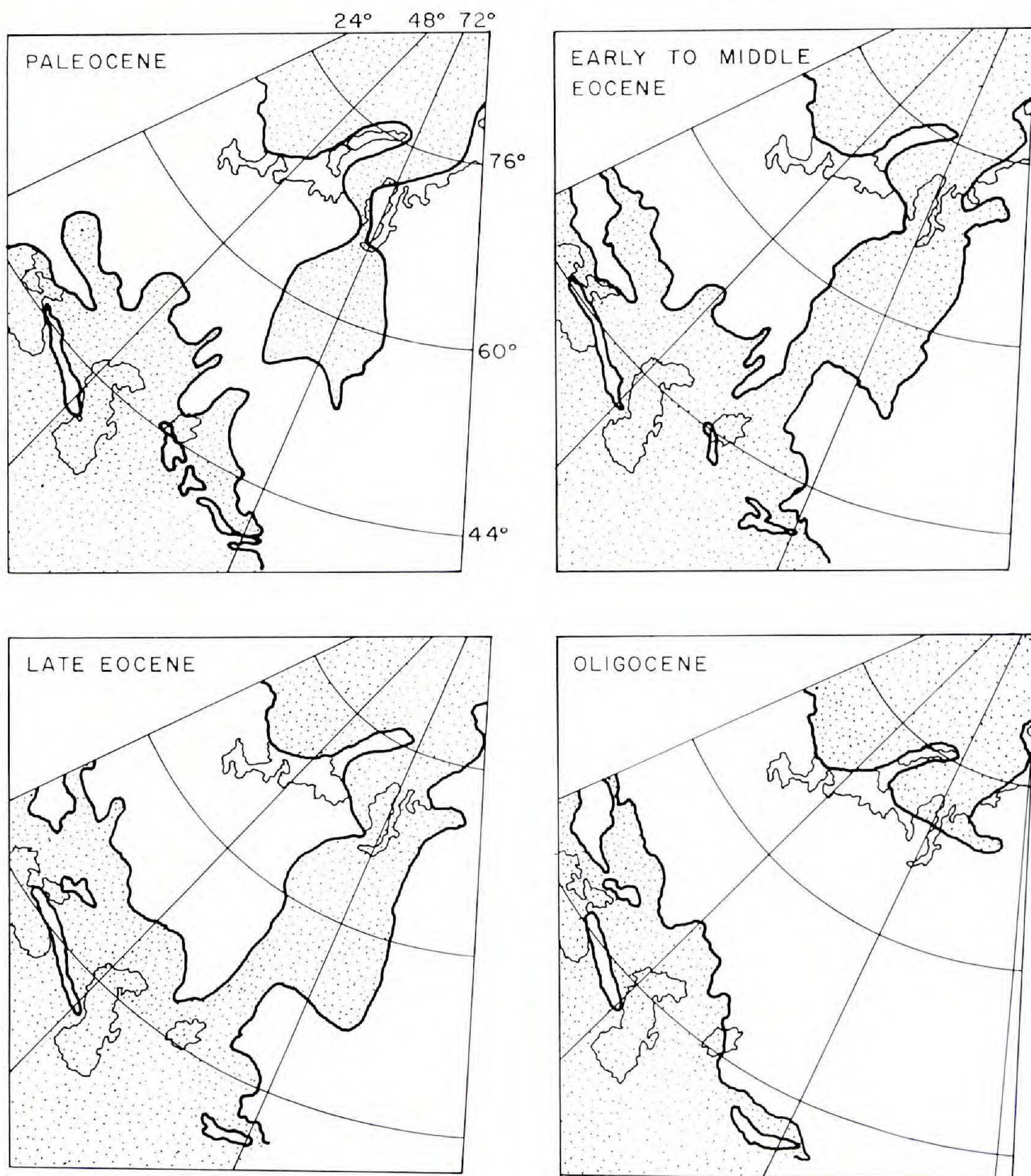
MAP 5. Sequential generalized paleogeography showing advance and retreat of Turgai Straits (shaded area) in central Asia from Paleocene through Oligocene time. Heavy lines = paleocoastlines, light lines = present coastlines. After Vinogradov (1967–1968).

EARLY TERTIARY FLORISTIC LINKS BETWEEN EUROPE AND EASTERN ASIA

If eastern North America shared an appreciable portion of the boreotropical flora with Europe, then some degree of the present similarity between the floras of eastern Asia and eastern North America must have involved early or middle Tertiary floristic exchange between Europe and eastern Asia. The evidence for a Tertiary European-Asian link is scattered. The Turgai Straits (MAP 5) separated Europe from western Siberia from the mid-Mesozoic to the end of the Eocene and are generally presumed to have formed a biogeographic barrier to animals (Kurtén, 1966; Muller, 1970; McKenna, 1975, 1983a; Russell, 1975; Hoch, 1983), although the severity of this barrier has been disputed (Savage & Russell, 1983). Its effect on plants is unclear. This seaway may have been

bridged intermittently in the Eocene, linking western Siberia with Fennoscandia (Russell, 1975; Heissig, 1979; Chow & Zheng, 1980; McKenna, 1983a, 1983b). According to McKenna (1983a), Fennoscandia and southwestern Europe were not directly linked in the Paleocene and Eocene (but note the different opinion of Plaziat (1981) mentioned above). If so, biotic exchange between western Siberia and southwestern Europe in the Eocene would have involved dispersal from Fennoscandia to Greenland via the DeGeer route, and then from Greenland to southwestern Europe by the Thulean route—a roundabout track, and one crossing several climatic zones. There is no particular plant evidence applicable to this possibility. The final closure of the Turgai Straits commenced in the Early Oligocene, initiating an influx of Asiatic and southeastern European vertebrate taxa into southwestern Europe (but see Heissig, 1979, who believes that the influx is largely Balkan in origin, coming up connected islands in the Tethys from the southeast).

This resulted in what Stehlin (1909) termed the "Grande Coupure," an Early Oligocene event in which roughly 50 percent of the preceding mammal fauna went extinct and was replaced by new taxa (McKenna, 1983b). The new mammals were presumably accompanied by new plants, and indeed the Early Oligocene was a time of change and modernization of the western European flora, although the details of this transition have not been worked out.

Probably the most important avenue of dispersal of the boreotropical flora across Eurasia involved the Tethys Seaway, which has shaped the present and past distributions of a variety of organisms (e.g., corals and seagrasses (McCoy & Heck, 1976), and echinoderms (Ali, 1983)). The classic boreotropical assemblage is the London Clay Flora, located on the "midpoint" of the Eocene Tethys Seaway (MAP 6). Floras of similar composition exist in the Eocene of central Europe (Palamarev, 1973) and in the Eocene and Oligocene of Egypt (Chandler, 1954; Bown *et al.*, 1982). A single fruit of *Anonaspermum* Reid & Chandler from the Paleogene of Pakistan (Tiffney, unpubl. data) hints at the further eastward extension of elements of this flora. It is unclear how far east along the Tethys the flora ranged. McKenna (1983b) notes that the Paleocene terrestrial faunas of China (C. K. Li & Ting, in press) are quite distinct from those of the rest of the Northern Hemisphere, suggesting a distinct biotic province at the eastern end of the Tethys in the earliest Tertiary. Thus, although the Eocene flora of western Europe is similar to the modern flora of Southeast Asia, it may have been less so to the Eocene floras of Southeast Asia. The similarity between the extant floras of eastern Asia and the Tertiary floras of Europe continued through the latest Tertiary, often involving similarity on the species level in the later Miocene and Pliocene (Tralau, 1963). This suggests that some amount of European-Asian interchange occurred after the decline in importance of the North Atlantic land bridge, and even as the Tethys Seaway began to fragment.

ORIGINS AND DIRECTIONS

This discussion has often implied a place of origin and a direction of subsequent spread of the boreotropical flora. This is a complex topic and is treated
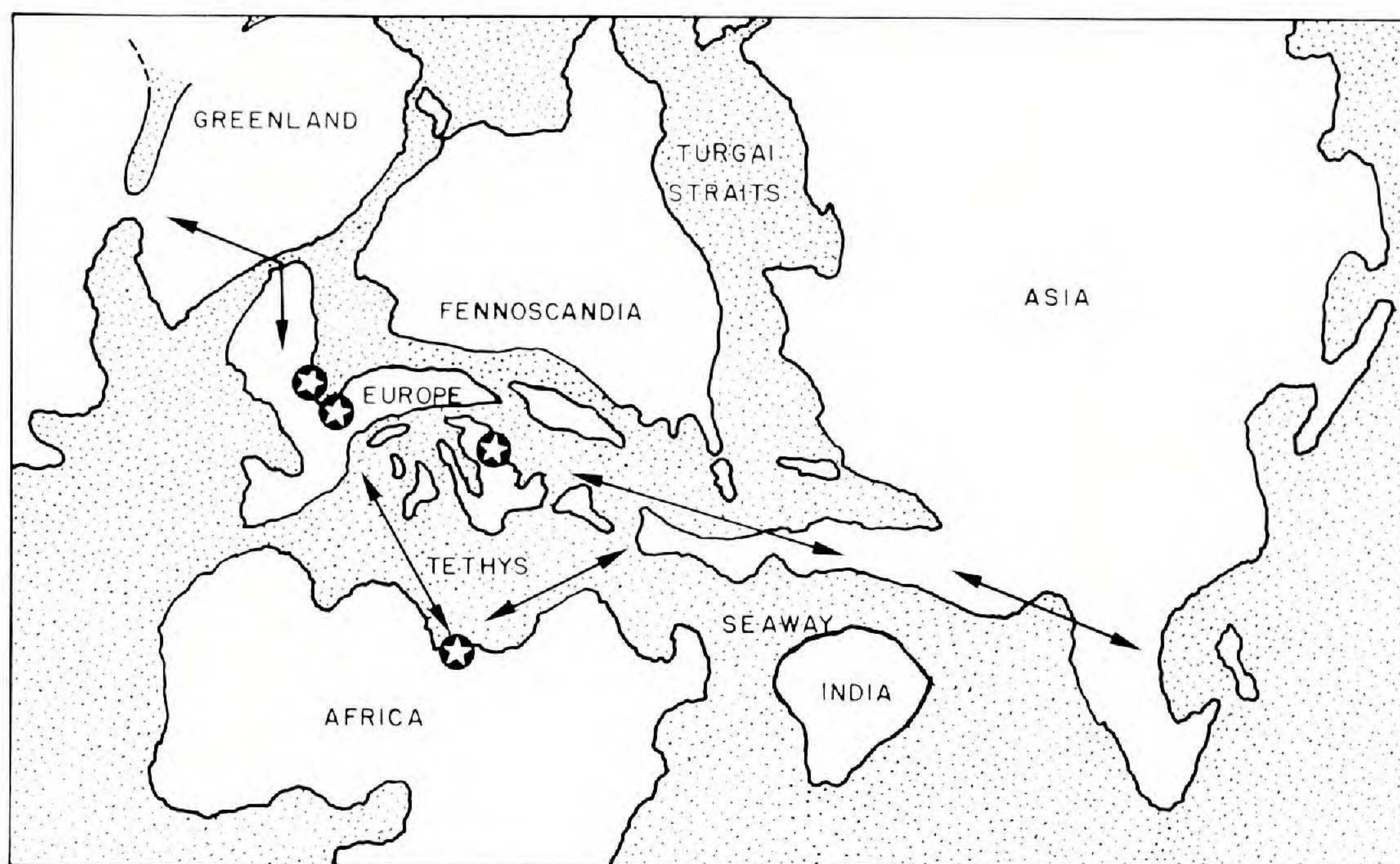
MAP 6.   Generalized paleogeography of the Tethys Seaway, Early to Middle Eocene, showing possible routes of movement of boreotropical flora along seaway (arrows) and known occurrences of floras similar to that of London Clay (stars). Assembled from, but not necessarily adhering to, data from Vinogradov (1967–1968), Smith *et al.* (1973), Novodvorskaja and Janovskaja (1975), Pożaryska and Cuik (1976), Smith and Briden (1977), Pożaryska (1978), Heissig (1979), Buchardt (1981), Plaziat (1981), Srivastava *et al.* (1981), Parrish *et al.* (1982), Pomerol (1982), and McKenna (pers. comm.).

separately (see Tiffney, 1985), but certain aspects of it require consideration here.

The boreotropical flora could have evolved in tropical, temperate, or polar regions during the early Tertiary. Our present knowledge of the Tertiary paleobotanical record of the tropics is too poor to provide any but the most speculative evidence. Knowledge of temperate regions is far better, but even with the information available we lack the temporal resolution to determine place of first appearance. Knowledge of the boreal zone is limited but contributes some information. Contrary to the geofloral hypothesis (e.g., Axelrod, 1966), the Late Cretaceous–early Tertiary North Pole is not an important center of origin. Instead, it appears to have supported a species-poor flora of deciduous taxa (see Wolfe, 1977; Hickey *et al.,* 1983; Hickey, pers. comm.), several members of which intermingled with the boreotropical flora when it appeared. However, this deciduous polar forest generally appears to have remained to the north of the boreotropical forest. Thus, although these deciduous taxa played a part in the boreotropical forest, the Beringian and/or Atlantic land bridges cannot be considered the points of origin of the boreotropical flora but only as passageways in its spread.

Spread implies direction. However, I do not believe that it is presently possible to trace the direction of spread of elements of the boreotropical forest across any of the bridges or barriers discussed above. For this reason I have attempted to describe biogeographic corridors in a neutral manner; if any

phraseology in the preceding seems to imply directionality, it is unintentional. It is quite likely, however, that spread will ultimately be found to involve the movement of different lineages at different times by different routes (see Tiffney, 1985). Elucidation of this assumption will only follow from careful biogeographic analysis of individual plant taxa. The use of cladistic methodology in this study (e.g., Donoghue, 1983a, 1983b, for *Viburnum*) may be very useful in demonstrating the geographic history of movement within or between taxa.

POST-EOCENE HISTORY OF THE BOREOTROPICAL FLORA IN EASTERN NORTH AMERICA

If the boreotropical flora had full access to eastern North America in the Early Eocene, the question remains as to whether its lower current diversity is a function of the Eocene-Oligocene climatic deterioration, of the Pleistocene deterioration, or of a combination of the two. Wang (1961) and Wolfe (1977) suggested that the Eocene-Oligocene climatic deterioration caused outright extinction of many boreotropical taxa, including the majority of the thermophilic elements, in eastern North America. Wolfe further suggested that the subsequent diversification of the eastern North American mixed mesophytic forest was restricted by the absence of these thermophilic evergreen taxa. This is in contrast to the situation in western North America, where a residual evergreen vegetation contributed greatly to the growth in diversity of the mixed mesophytic forest in the Miocene (Wolfe, 1969, 1977). Perhaps the only fossil evidence that bears on this supposition is that of the Brandon Lignite. The age of the deposit is presently accepted as post-Eocene (Wolfe & Barghoorn, 1960; Frederiksen, 1984 and pers. comm.), although Berry (1919) once suggested that it was Eocene. This flora includes several thermophilic boreotropical taxa (e.g., *Euodia, Alangium, Turpinia*) no longer extant in eastern North America. This implies that—at least in some portion of eastern North America—boreotropical elements survived the Late Eocene–Early Oligocene climatic deterioration but went extinct in the later Tertiary or Quaternary.

Although it is not presently possible to indicate a particular period of time for this extinction, suggestions can be made as to why extinction had a stronger effect in eastern North America than in eastern Asia. Eastern North America is geographically smaller than eastern Asia and would be expected to have a smaller flora measured on a species per area basis. The lower topography of eastern North America offers a more limited range of habitats than is encountered in eastern Asia (Wolfe, 1977). Further, the Appalachian Mountains are oriented north–south, and in conjunction with the Mississippi River valley, they provide a geographic funnel conveying cold Arctic air masses directly to the Caribbean. This contrasts with the geography of eastern Asia, where many of the mountain ranges serve as shields from cold air masses. As a result, locations in eastern North America and eastern Asia may have similar mean monthly minimum temperatures, but the absolute minima in North America are considerably lower (Wolfe, 1979). Finally, starting in the Middle Eocene, the rain shadow of the western mountains of North America created a barrier of dry environments in central North America. The southerly extent of this

barrier, and its effect on floristic exchange between southeastern North America and the highlands of Mexico and Central America, is unclear. Boreotropical elements are known from the Oligocene of Puerto Rico (Graham & Jarzen, 1969). Temperate elements of the boreotropical flora were present in Mexico in the Middle Miocene and appear to have moved southward in the later Tertiary (Graham, 1973, 1976). The history of more thermophilic boreotropical taxa in this area is unknown. It is possible that the zone of central North American dry climates caused the extinction of those boreotropical taxa forced southward by winter temperature extremes. Although this situation would have been most dramatic in the Quaternary (e.g., Delcourt & Delcourt, 1981), similar events could have occurred earlier in the Tertiary, incrementally curtailing the floristic diversity of eastern North America. Like the biogeography and environments of the mid-continental area in the early and middle Tertiary, those of the southeastern United States and northern Central America offer fertile ground for synthetic inquiry.

In conclusion, the Eocene-Oligocene climatic deterioration may have influenced the diversity of the eastern North American boreotropical flora, but it did not decimate the flora. The specific pattern and timing involved in the depauperization of the eastern North American flora during the later Tertiary cannot be discerned at this time.

SUMMARY

The early Tertiary boreotropical flora of eastern North America was probably as diverse as that of any other portion of the contemporary Northern Hemisphere. This conclusion is supported by limited paleobotanical data from eastern North America and the strong paleozoological and paleogeographic evidence that eastern North America and southwestern Europe were linked by North Atlantic land bridges in the latest Paleocene or the earliest Eocene when the boreotropical flora was reaching its maximum extent.

Western North America and eastern Asia probably derived their shared component of the boreotropical flora by both the Atlantic and Bering land bridges; the relative contribution of each is unclear at this time. The potential for early Tertiary floristic exchange between eastern and western North America is an important question for which few data exist. Although dry environments may have been present in central North America by the Middle Eocene, they may have been broken by bands of forest or by riverine gallery forests.

The similarities of the modern floras of eastern Asia and eastern North America are probably due to an early Tertiary linkage between the two areas involving the North Atlantic land bridges and Europe. However, the flora of eastern North America cannot be considered as solely the product of exchange across a North Atlantic bridge; it is a composite of elements derived from Atlantic, Polar, Mexican and Central American, and western North American sources, in which the Atlantic element may dominate. This assumption can be tested by careful examination of European and eastern and western North American fossils in light of modern taxa of eastern North America, Mexico and Central America, and Asia. This implies that modern systematists studying

plants with Tertiary relict distributions must consider that eastern North America may have harbored phylogenetically distinct and important taxa in the Tertiary, but that these are now extinct.

The present lower diversity of the flora of eastern North America relative to that of eastern Asia appears to be a "post-boreotropical flora" phenomenon. The geography of eastern North America is less diverse than that of eastern Asia and favors greater winter extremes. Further, a moisture barrier may occasionally or consistently have separated eastern North America from Mexico and Central America. As a result of these features, the mid- and late Tertiary derivatives of the boreotropical flora in eastern North America suffered greater extinction than did their counterparts in eastern Asia. The timing of this extinction in eastern North America (later Tertiary or Quaternary) is not clear from present evidence.

ACKNOWLEDGMENTS

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